

**OVIPOSITION BEHAVIOR OF THE APPLE BLOTCH  
LEAFMINER, *PHYLLONORYCTER CRATAEGELLA*  
(CLEMENS) (LEPIDOPTERA: GRACILLARIIDAE)**

THOMAS A. GREEN AND RONALD J. PROKOPY

Department of Entomology, University of Massachusetts,  
Amherst, Massachusetts 01003

*Abstract.*—Observations of oviposition by apple blotch leafminer moths, *Phyllonorycter crataegella* (Clemens), on apple foliage in the field and in the laboratory indicated oviposition occurred solely on the undersides of leaves, and primarily on the middle third of the leaf (between petiole and apical tip), midway between the mid-vein and margin. A stereotypical sequence of events lasting ca. 1 min was observed prior to egg deposition. This included walking while tapping the leaf underside with the antennae, probing a small area (ca. 1 cm<sup>2</sup>) of the leaf with the ovipositor, and violent side-to-side shaking of the abdomen at egg deposition. Results of choice tests in the laboratory suggest apple blotch leafminer moths do not discriminate against oviposition sites previously occupied by freshly deposited conspecific eggs. Our results indicate commercial apple growers may improve control of this pest by applying adulticides just prior to or during the first warm, calm evening in early spring when foliage and leafminer adults are present.

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The apple blotch leafminer, *Phyllonorycter crataegella* (Clemens) (ABLM), one of several gracillariid species infesting apple in North America, is distributed throughout much of New England, west to the Hudson River Valley, and south to Virginia (Beckham et al., 1950; Weires et al., 1980; Coli and Prokopy, 1982; Maier, 1983; Van Driesche and Taub, 1983). It parasitizes at least 17 host plants in 7 genera in New England (Maier, 1985). The ABLM completes three generations per year, with the first adults emerging in early spring from pupae in the previous season's leaves. Female ABLM deposit eggs singly on the undersides of host leaves from mid- to late afternoon until dark (Green and Prokopy, 1984). Adult ABLM and larval mines are concentrated in the lower part of apple tree canopies in commercial orchards during the first generation, spreading upwards in succeeding generations (Beckham et al., 1950; Green et al., 1987).

ABLM has achieved major pest status in commercial apple orchards in New York and New England over the past 13 years due to its development of resistance to organophosphate insecticides (Weires, 1977; Weires et al., 1982; Van Driesche et al., 1985). Heavy infestations can cause premature fruit ripening and drop, reduced fruit size and reduced fruit set the following season (Reissig et al., 1982). The oviposition behavior of this insect may have important implications for pest management programs (Green et al., 1987).

Competition for resources could be more important for leaf-mining insects than for species that are more mobile in larval stages (Bultman and Faeth, 1985), as leafminers typically spend their entire larval life within one leaf or portion of a leaf. Intraspecific competition has been demonstrated for other leaf-mining insects (Parel-

la, 1983; Quiring and McNeil, 1984; Potter, 1985), including gracillariid species (Martin, 1956; Bultman and Faeth, 1986).

If competition is important, evolution may favor the development of mechanisms allowing individuals to detect and avoid resources already occupied by conspecifics (Prokopy, 1972; McNeil and Quiring, 1983; Prokopy et al., 1984). Some of these mechanisms may have potential in pest management programs (Prokopy, 1981; Roitberg and Prokopy, 1987).

The objectives of the following study were to describe the oviposition behavior of female ABLM, and examine possible discrimination against host leaves previously occupied by conspecific eggs.

#### MATERIALS AND METHODS

All observations of ABLM oviposition in the field (experiment 1) were conducted in commercial apple orchards in New England during 1983 and 1984, as part of a larger study of ABLM behavior (Green and Prokopy, unpubl. data). An area within the canopy of an apple tree was selected at random, and the undersides of leaves were searched until an ABLM adult was located. The activity of the moth was recorded for 5 min, or until the moth flew out of sight of the observer. We recorded the number of ovipositions, leaves visited, repeat visits to the same leaf, and whether a moth arrived on a leaf by flight or by walking.

ABLM observed in the laboratory (experiments 2, 3, 4) were collected as pupae in leaves from commercial apple orchards in western Massachusetts. The portions of leaves containing mines were held individually in 30 ml plastic cups until adult emergence. Upon emergence, males and females were placed collectively in a 3.8 l glass jar, the opening of which was covered with organdy cloth to permit air circulation. Each morning, mating pairs were removed from the jar and placed in the cups until females were used for experimentation the following day. Throughout, ABLM adults were provided free access to spring-water-soaked dental wicks, and maintained under natural lighting in front of a large screened window. All laboratory experiments, conducted on a table placed in front of this window, occurred from 1600–2100 hours (Eastern Standard Time), the time of peak ABLM oviposition in the field (Green and Prokopy, unpubl. data).

Foliage used in laboratory experiments was collected daily from unsprayed apple trees and carefully examined to exclude leaves with leafminer eggs or larval mines. Only basal leaves (or fruit cluster leaves, experiment 4) of growing terminals were selected for use in the choice tests to provide uniform leaf age and quality. Leaves were maintained on the terminals, held in water-filled vials. Average leaf size in experiments 2 and 3 was 6.2 by 4.2 cm.

During the summer of 1984, 23 ABLM were observed individually in the laboratory for 3 hr each (experiment 2). Each moth was held in a vertical cylindrical cage of clear acetate (14 cm diameter, 25 cm height), containing an apple terminal with 8 leaves. The base of the terminal extended through a hole in the floor of the cage (a plastic petri dish bottom) into a vial containing water. The top of the cage was covered with organdy cloth to allow air circulation. ABLM females were placed singly in a stoppered vial within the cage, and were allowed to acclimate for 5 min before the cotton stopper was removed (remotely, by pulling a string) and observations were



begun. The number and sequence of leaf visits, number and location of ovipositions, and the sequence of behaviors involved in oviposition were timed and recorded. After 3 hours, the moth was removed from the cage. The number of ovipositions was confirmed by examination of leaves under a microscope, and the length and width of each leaf was measured and recorded. The location of the first egg only (to eliminate any influence of previous ovipositions) on each leaf was plotted according to distance from petiole, margin, and midrib.

In experiment 3, conducted during the summer of 1984, individual ABLM females (caged as in experiment 2) were provided with a terminal of 2 leaves, one containing 1 or 8 ABLM eggs (oviposited <30 hr previously) and one without prior ovipositions (=clean). Each female was observed 30 min or until the first oviposition. Each female was pre-tested by being allowed to oviposit freely on a clean leaf until it left the leaf. Only females which oviposited at least once in the pretest were used in the experiment.

In experiment 4, conducted in July of 1987, individually-caged ABLM females were provided with 2 small leaves (average size 2.3 by 1.4 cm), one clean and one with 1 or 2 prior ovipositions. The leaf half (right or left of the midvein) containing or receiving eggs was noted. ABLM females were pre-tested by being offered 3 pairs of clean leaves in succession, the next pair being offered after one oviposition. Only females which oviposited three times prior to the assay were used.

#### RESULTS

In commercial apple orchards, 25 ABLM females were observed exhibiting oviposition behavior (Table 1), all between 1645 and 2035 hours. Of the 25, 8 moths were observed probing the leaf underside with the ovipositor but did not oviposit while under observation. All ovipositions occurred on the undersides of leaves, though arrival was on the upper surface of leaves in about half of all visits (N = 102 total visits). Overall, 19.1% of leaves visited received an egg, and 8.8% of all leaf visits were repeat visits by the same female to the same leaf. No moths oviposited more than once per leaf visit. In one instance a second egg was placed on a leaf previously oviposited on by the same female during a prior visit. About two-thirds of leaf visits were via walking from the stem or adjacent leaves (Table 1), and about one-third were by flight.

Repeated attempts to observe oviposition in the laboratory under artificial lighting were unsuccessful, although females confined for several days with foliage under those conditions did eventually oviposit. We succeeded in observing oviposition by offering foliage to females in front of a screened window, under natural lighting, temperature, and humidity, and during the time period within which oviposition occurs in the field.

Of the 23 moths observed in the laboratory for 3 hr, 19 visited foliage and 15 oviposited at least once, for an overall average of 6.7 eggs per female (range = 0–20). After tarsal contact with a leaf, females spent an average of 30 s ( $\pm 3.1$  s, SE) walking on the leaf, during which they continuously tapped the leaf surface with the antennae, gradually narrowing down the area “searched” by walking in an increasingly tighter circle. Once ovipositor contact with the leaf occurred, females spent an average of 29 s ( $\pm 3.4$  s) probing a small area of the leaf (ca. <1 cm<sup>2</sup>) with the ovipositor, often taking short, backward steps. This period ended with the abdomen bent at a

Table 1. Observations of ABLM exhibiting oviposition behavior (=ovipositor in contact with leaf) in commercial apple orchards in New England, 1983–1984.<sup>a</sup>

	Mean per moth ( $\pm$ SE)
Minutes observed	3.7 $\pm$ 0.69
Number leaf visits	4.1 $\pm$ 0.52
Number different leaves visited	3.8 $\pm$ 0.47
Number ovipositions observed	0.8 $\pm$ 0.62
	Proportion $\pm$ SE
Proportion leaves visited	
By walking	69.6 $\pm$ 0.01
By flight	30.4 $\pm$ 0.01

<sup>a</sup> Twenty-five moths were observed individually for 5 min or until leaving sight of observer. Data include 9, 12 and 4 ABLM during first through third generations, respectively.

near 90° angle to the rest of the body and the ovipositor firmly planted against the underside of the leaf. The female then shook violently 3–5 times from side to side, for a total of about 1 s, after which time the egg was deposited on the leaf surface. The moth then quickly lifted the abdomen and ovipositor off the leaf surface, and crawled away from the egg an average of 13.1 s ( $\pm$ 3.4 s) after the ovipositor was firmly in place on the leaf underside.

On the first leaf visit by laboratory-observed moths, females frequently oviposited more than once before leaving (mean 1.7 eggs/first leaf visit/female). They did so much less frequently on subsequent leaf visits (mean 0.7 eggs/leaf visit/female). Among the 15 replicates in which oviposition occurred, 78% of leaf visits did not result in an oviposition.

Females oviposited significantly more eggs ( $P < 0.5$ ,  $G$ -test, Sokal and Rohlf, 1981) on the middle of three lateral sections of the leaf (sectioned perpendicular to mid-vein, Fig. 1a), and the second and third quarters longitudinally (sectioned parallel to mid-vein, Fig. 1b). Among the 8 leaves on each terminal, no preference was exhibited for any particular leaf position relative to the most basal or apical leaf.

In experiment 3, no significant differences were detected in the number of new ovipositions on clean leaves vs. leaves with one ( $N = 26$ ) or eight prior ovipositions ( $N = 29$ ), although substantially more new eggs were placed on clean leaves vs. leaves with 8 prior ovipositions (19 vs. 10, respectively). ABLM females oviposited on the first leaf visited (53 of 55 replicates, or 96%), regardless of the presence or absence of prior ovipositions. For some unknown reason, ABLM females were not nearly as selective as they were in the field or in experiment 2, where only 19% and 32% of leaf visits resulted in oviposition, respectively.

Resolving these concerns was the rationale for the final experiment, in which small leaves were used and the leaf-half receiving the new egg was noted (Table 2). By restricting the amount of leaf area available and comparing oviposition on the basis of a portion of the leaf, discrimination by females against small occupied areas of the leaf might become apparent. Pretesting each female on 3 clean leaves (vs. only 1 in experiment 3) was intended to accentuate “choosiness” by reducing any effect of oviposition deprivation and by providing uniform pre-assay oviposition experience which could be necessary for recognition of conspecific eggs or host markers.



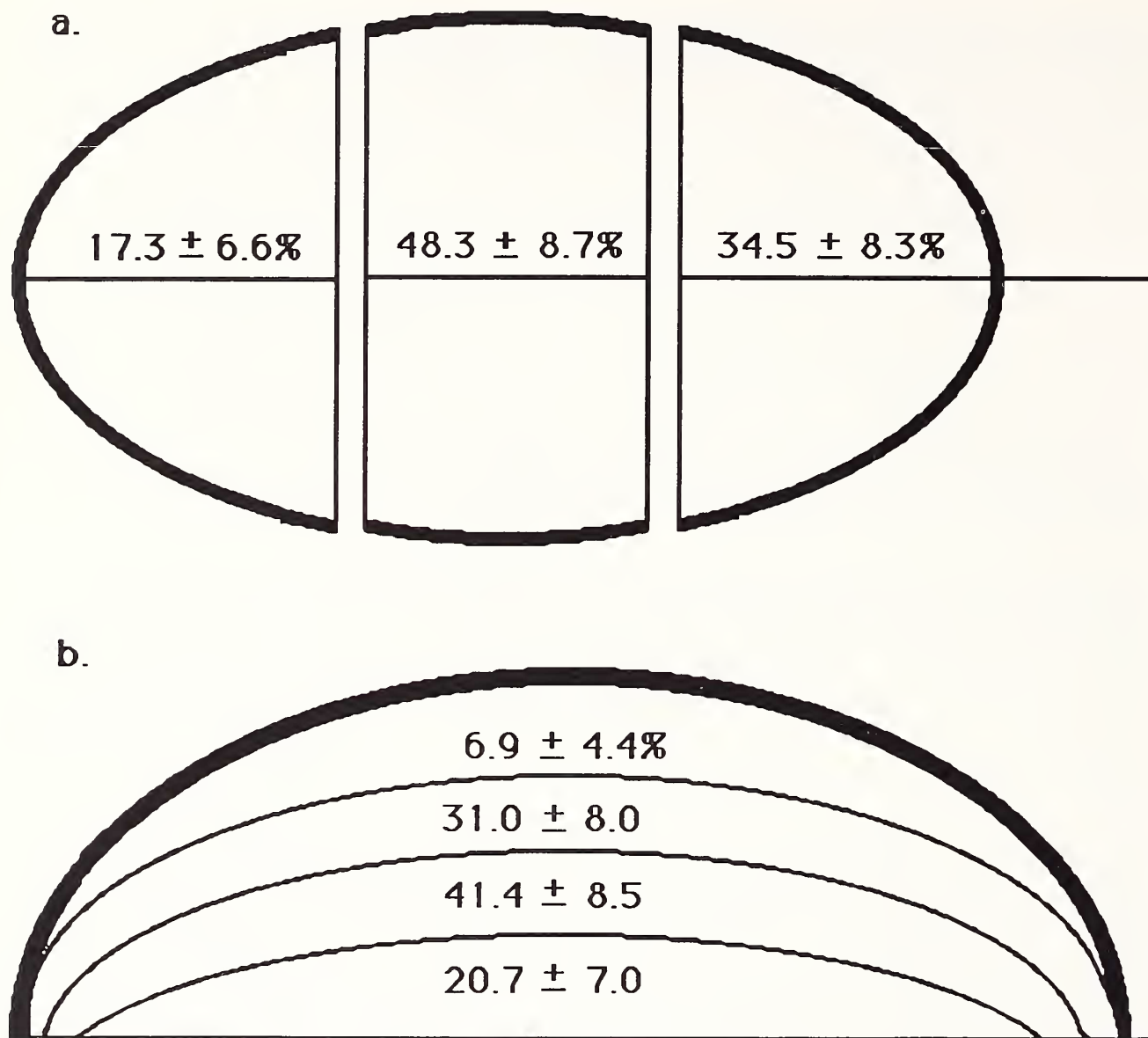


Fig. 1. Lateral (a) and longitudinal (b) distribution of ABLM eggs according to leaf surface area  $\pm$ SE. Eggs deposited during 3 hr observations in laboratory. Only the first egg deposited on any leaf was included, N = 58 eggs, 15 moths.

“Choosiness” was greater in this experiment (56% of leaf visits resulted in an oviposition) than in experiment 3, but still not equal to levels observed in orchards or in experiment 2. The first leaf visited received the first oviposition in 56% of all replicates.

No discrimination was detected against entire leaves or leaf halves containing one or two previous ovipositions. Leaves with one prior oviposition received new eggs as often as did clean leaves (Table 2). Of the 14 new eggs placed on leaves with a prior oviposition, 7 were placed on the same half (right or left side of the mid-vein) of the leaf underside as the initial egg. Leaves with 2 prior ovipositions received significantly more new eggs than did clean leaves.

#### DISCUSSION

Results of this study agree with observations by Beckham et al. (1950) of a concentration of oviposition by ABLM on the mid-section of the leaf. Pottinger and

Table 2. Comparison of oviposition by individually caged ABLM females provided with 2 leaves, one free of conspecific eggs (=clean) and one with 1 or 2 ABLM eggs deposited <30 hr previously. For leaves with prior oviposition, comparison is between halves of leaves (leaf divided by the midvein) receiving the new egg.

Treatment	N	Leaf receiving new egg <sup>a</sup>	
		With egg(s)	Clean
1 previous egg	28	14a	14a
2 previous eggs	13	11a	2b
		Leaf half receiving new egg	
		Half with egg(s)	Clean half
1 previous egg	14	7a	7a
2 previous eggs	7	5a	2a

<sup>a</sup> First egg on leaf only. ABLM were allowed a single oviposition on each of 3 clean leaves <30 min prior to testing. Data within a row and followed by the same letter are not significantly different ( $P > 0.05$ ,  $G$ -test, Sokal and Rohlf 1981).

LeRoux (1971) found no preference for the proximal or distal leaf half in a related species, the spotted tentiform leafminer (STLM), *P. blancardella* (F.), but they did not report distribution by thirds as presented here. Otherwise, their description of oviposition behavior is similar to what we observed in ABLM. They speculated that the violent side-to-side shaking by females immediately prior to egg deposition might clear the leaf surface and/or ready the egg for deposition.

The extent and importance of inter- and intraspecific competition in regulating natural populations has been a topic of considerable interest in the recent literature (Lawton and Strong, 1981; Schoener, 1982, 1983). Intraspecific competition for larval resources is unlikely in leafminer populations maintained at low densities by natural enemies (Faeth and Simberloff, 1981). Regulation of ABLM population densities by parasites has been noted by many workers (Dean, 1940; Gambino and Sullivan, 1982; Maier, 1982; Van Driesche and Taub, 1983; Van Driesche et al., 1985; Drummond et al., 1985). However, competition might occur, even at low ABLM densities, if the supply of superior leaves or portions of leaves is limiting.

As in most but not all lepidopteran leafminers (Gross, 1986), the ABLM is restricted for its entire larval life to one portion of a leaf (larvae do not cross major leaf veins), chosen by the female adult. Results of this and previous studies indicate ABLM females oviposit preferentially on the mid-section of leaves, within the interior half of the tree canopy throughout the season, and in the lower portion of the canopy during the first generation (Beckham et al., 1950; Green and Prokopy, unpubl. data). This part of the canopy may be preferred due to less wind interference with oviposition, closer proximity to emergence sites (Beckham et al., 1950), or a reduced tendency for interior leaves to abscise prior to completion of larval development (Bultman and Faeth, 1986b).

Other factors that might limit availability of favorable oviposition sites include the lesser amount of apple foliage in early spring and proximity to shelter (Martin, 1956). Selection of leaves by leafminers according to leaf size (Bultman and Faeth, 1986a), nutrient content, or exposure to the sun (Faeth et al., 1981), or selection against leaf noxious compounds or damaged leaves (Faeth, 1985) may also occur.



The "choosiness" of ABLM noted here (i.e., visiting many leaves without ovipositing, Table 1), suggests that these or other factors may operate in ABLM oviposition site selection.

Restricted availability of superior oviposition sites may lead to over-utilization of existing sites. Interference competition among larvae, including cannibalism, has been demonstrated in other gracillariids, including STLM (Pottinger and LeRoux, 1971) and the aspen blotch leafminer, *P. salicifoliella* (Chambers) (Martin, 1956), and in the dipteran leafminers *Agromyza frontella* (Rondani) (Quiring and McNeil, 1984) and *Liriomyza trifolii* (Burgess) (Parrella, 1983). Interference competition without cannibalism has been observed in another dipteran, the native holly leafminer, *Phytomyza ilicicola* Loew (Potter, 1985). Besides cannibalism, the presence of conspecifics may also result in a general depletion of resources, leaf abscission, or in induction of plant defenses.

Possible restricted availability of favorable oviposition sites, limited mobility of ABLM larvae and adults (Beckham et al., 1950; Green and Prokopy, 1986), and relatively permanent host plants (present over 3 generations) are ecological characteristics which have been positively correlated with host marking ability, used to avoid reduced fitness or mortality due to overcrowding in other species (Prokopy, 1981; Roitberg and Prokopy, 1982, 1987). The broad host range of ABLM (17 species, Maier, 1985) is one characteristic not generally found in species which mark hosts. Given the concentrated searching behavior by ABLM prior to oviposition coupled with the presence of ABLM eggs on the surface of the leaf (as opposed to eggs inserted internally), host marking may not be required for ABLM to recognize previously occupied sites. Energetic costs and potential costs due to use of host-marking cues by natural enemies may outweigh any benefits (Roitberg and Prokopy, 1987).

Oviposition twice on the same leaf by a single female in the field (experiment 1), lack of discrimination by ABLM females against leaves with one egg (experiment 3), concentrated "searching" behavior over a small leaf area prior to oviposition in the lab (experiment 2) and the ability of a single apple leaf to support several ABLM larvae (Reissig et al., 1982) suggest that the biologically significant unit chosen for egg laying by a female may be a portion of the leaf rather than the entire leaf. The substantially though not significantly greater new oviposition on clean leaves vs. leaves with 8 prior ovipositions (experiment 3) suggested possible discrimination on the basis of prior egg density. However, in all but 2 of the replicates, the first leaf visited received the first oviposition. Any discrimination against the leaves with 8 prior ovipositions would have been on the basis of cues other than contact with the leaf or eggs.

The significant preference for leaves with 2 prior ovipositions suggests that some other factors, possibly related to leaf quality per se, may be more important in ABLM selection of leaves for egg laying than the presence of conspecific eggs, or that clumping of eggs may be advantageous. Alternative hypotheses for the apparent failure of ABLM females to discriminate against previously egg-occupied host leaves or parts of host leaves include (1) reduced "choosiness" in this assay; (2) discrimination only at egg densities greater than those tested, or only against sites occupied by larvae or by eggs that are more mature; (3) a conspecific egg recognition/discrimination system may not have developed in ABLM because of insufficient selection pressure for such a system.

ABLM mate at temperatures at least as low as 7°C (Green and Prokopy, unpubl. data), but oviposition by ABLM and STLM may be restricted to periods of higher temperature (>9–15°C) and low wind speeds (Trimble, 1986; Green and Prokopy, unpubl. data). Therefore, a considerable buildup of mated female ABLM in sheltered locations may be possible until conditions are appropriate for oviposition. Once these conditions occur, ABLM females are capable of ovipositing up to 20 eggs each (average = 6.7 eggs per female) during a single 3-hr period. Thus, when needed, orchardists should apply adulticides against ABLM just prior to or during the first warm (>9–12°C), calm evening in the spring when foliage and ABLM adults are present.

Aspects needing additional work include examination of the distribution of ABLM eggs and larvae in the field for clumped, random or uniform dispersion, density dependent effects on larvae occurring from presence of conspecifics on the same leaf or different leaves on the same tree, and possible discrimination by ovipositing adults against leaves or portions of leaves occupied by larvae or by more mature conspecific eggs.

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